

Invasive catfish in northern Italy and their impacts on waterbirds

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Academic editor: Tim Blackburn | Received 13 January 2022 | Accepted 4 March 2022 | Published 25 March 2022

Citation: Milardi M, Green AJ, Mancini M, Trotti P, Kiljunen M, Torniainen J, Castaldelli G (2022) Invasive catfish in northern Italy and their impacts on waterbirds. NeoBiota 72: 109–128. <https://doi.org/10.3897/neobiota.72.80500>

Abstract

Predatory fish have occasionally been observed preying on birds, sometimes repeatedly, but few studies were able to unravel the overall significance of avian prey in fish diet and the predation impacts on bird populations. We used a control/impact study setup, using a Nature Reserve in northern Italy and a nearby control area, to determine: 1) the contribution of waterbirds to wels catfish diet in the Reserve, 2) the population density of wels catfish in the Reserve and control area and 3) the potential impacts of waterbird depredation by wels catfish on waterbird population trends. Our stable isotope Bayesian mixing model indicated that birds contributed 12.2% (5–27.9%, 50% confidence interval) of the diet of large wels catfish (> 98 cm in total length). Large individuals constituted the majority of the population in the shoreline areas of the reserve in 2013–2019, where the population was stable despite control efforts. Numbers were below detectable levels in the control area. Large wels catfish consumed an average of 224, 148 and 187 kg of birds during the 2019 chick growing period, as estimated through three different bioenergetic models. Compared to the control area, mallard reproductive success was diminished in the Reserve, likely due to higher rates of fish predation, although effects were variable in different years. Overall, our data suggest that high densities of invasive wels catfish might impact waterbird reproductive success through predation on bird chicks, but further studies would be needed to reduce uncertainties related to the intrinsic variability of field ecology data. Our study constitutes a preliminary attempt to assess the potential of introduced wels catfish to affect the conservation value of waterbird protection areas, and should be repeated at broader spatial and temporal scales.

Keywords

Predation, pulsed resources, *Silurus glanis*, stable isotopes, waterbirds, wels catfish

Introduction

Wetland loss has been particularly severe in the Mediterranean Region, where habitat conservation is still at lower levels than in other areas of the world (Hoekstra et al. 2005; Leberger et al. 2020), highlighting the need to maximise the effectiveness of existing protection, especially in Italy (Maiorano et al. 2007). The limited ability of habitat protection to address and control other threats affecting species distributions and biodiversity (e.g. climate change, pollution, biological invasions) could be at the root of differences in protection performance between areas (Pavón-Jordán et al. 2015; Gaget et al. 2020). Invasive species often diminish the effectiveness of protected areas, particularly those aimed at birds nesting on islands, with a wide range of cascading effects (Fukami et al. 2006). Invasive aquatic species have also been highlighted as a threat to freshwater protected areas (Saunders et al. 2002). Invasive fish have been considered as particularly detrimental for amphibians via predation (Vredenburg 2004; Finlay and Vredenburg 2007; Pope 2008) and for birds via competition and habitat modification, especially invasive cyprinids (Bajer et al. 2009; Epanchin et al. 2010; Maceda-Veiga et al. 2017). Waterbirds are flagships for wetland protection (e.g. under the Ramsar convention) and invasive terrestrial predators, such as mammals, have often been controlled to improve the breeding success of waterbirds (Gilbert et al. 1996; Whitehead et al. 2008). However, as yet, little consideration has been given to the potential impact of invasive predatory fish on birds.

Predatory fish have been occasionally observed preying and sometimes focusing, on birds. In marine environments, the giant trevally (*Caranx ignobilis*) has been observed hunting sooty terns (*Onychoprion fuscatus*) in the Seychelles (Attenborough 2017). A species well-known for its dietary breadth, the tiger shark (*Galeocerdo cuvier*) has been found to prey on terrestrial birds (rather than seabirds) along the coast of Alabama, perhaps exploiting extreme weather events that force migrating birds to land on water (Drymon et al. 2019). Large freshwater predatory fish like the taimen (*Hucho taimen*) (Kottelat and Freyhof 2007), the murray cod (*Maccullochella peelii*) (Harris and Rowland 1996), the northern pike (*Esox lucius*) and the muskie (*Esox masquinongy*) can also hunt birds. Northern pike presence has been shown to drive the habitat choice and reproductive success of nesting ducks through predation, especially on ducklings (Dessborn et al. 2011), although this effect was not clear in earlier studies (Lagler 1956). In this context, stomach content analysis is unlikely to yield a significant answer, as it integrates fish diet over a limited timespan (Windell 1968) and would require extremely intensive field sampling to detect occasional prey, such as birds. Stable isotopes, on the other hand, have been routinely used to investigate diet, as they integrate information over a

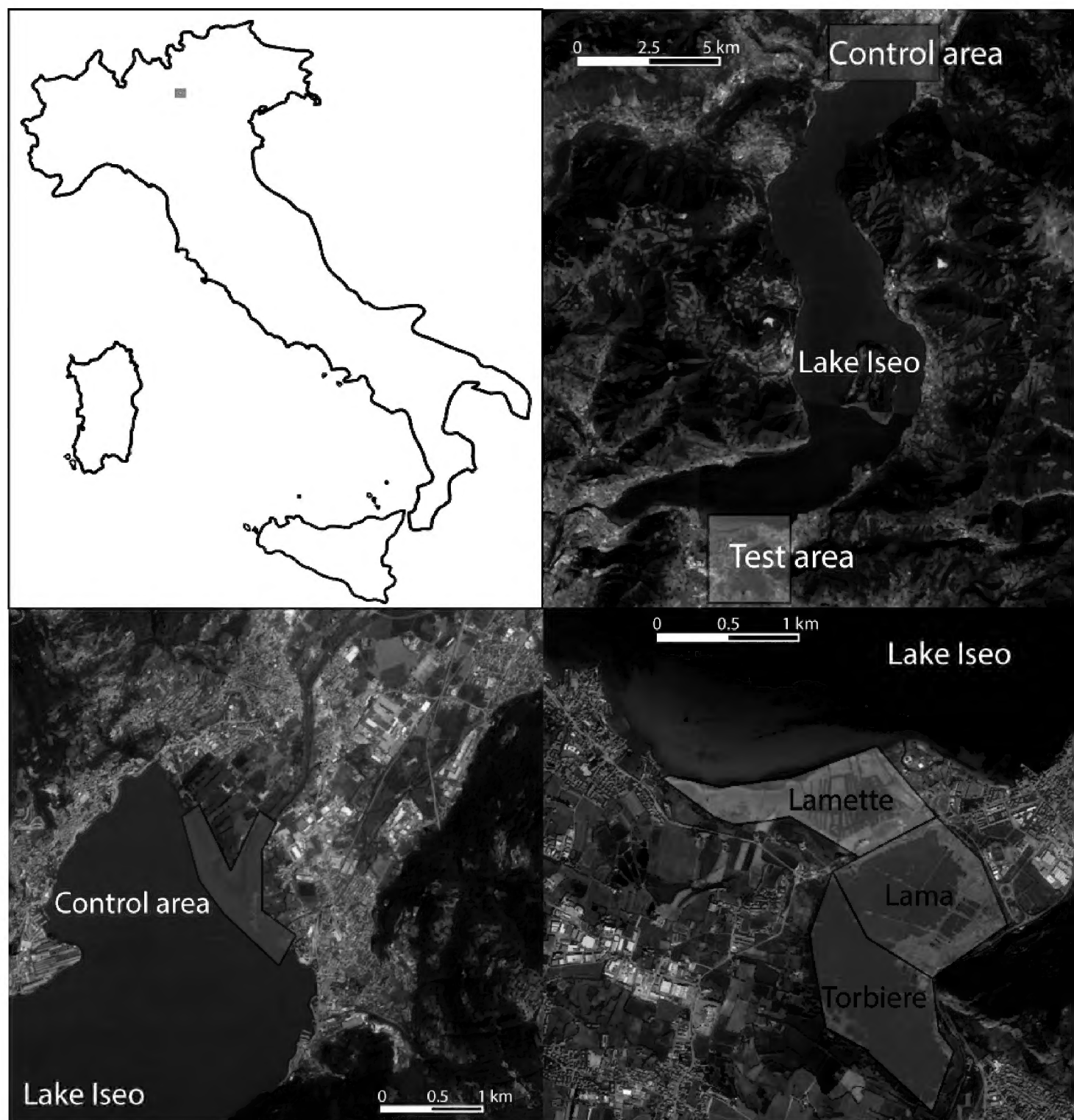


Figure 1. Location of the study area in Italy (upper left panel, in red) and location of the control (in green) and test (in orange) areas at the opposite ends of Lake Iseo (upper right panel). The lower left panel depicts the control area (in green), where the Oglio River enters Lake Iseo. The lower right panel depicts the test area, the Sebino Peat Bogs (*Torbiere del Sebino*), a Nature Reserve declared in 1984. Three different areas of the Reserve are named and shaded in yellow, blue and magenta, based on their depth, vegetation and numbers of human activities permitted. Satellite and aerial imagery are from Google Earth.

longer timespan (Perga and Gerdeaux 2005) without needing extensive sampling. Wels catfish (*Silurus glanis*) has been reported to feed on birds (Carol et al. 2009; Copp et al. 2009; Syväranta et al. 2010) and its large size makes it capable of preying on adults of large species, such as great cormorants (*Phalacrocorax carbo*, this study). Cucherousset et al. (2012) suggested that wels catfish are able to learn complex predation strategies, which were used to hunt bathing pigeons and showed that birds could reach 30–40% of the diet of specialised individual fish. However,

only one study attempted to unravel the overall significance of birds in wels catfish diet (Cucherousset et al. 2018) and its potential impacts on bird populations remains poorly understood.

Wels catfish is native to eastern Europe and western Asia and has been widely introduced to western Europe, where it quickly became invasive, but its impact on invaded ecosystems is still not fully understood (Copp et al. 2009). In Italy, wels catfish is now widespread, especially in the northern part of the country (Po River Basin). It grows faster than in its native range (Rossi et al. 1991) and has been highlighted as a potential driver of native fish decline (Castaldelli et al. 2013). We used a control/impact study setup, using a Nature Reserve in northern Italy and a nearby control area, to determine: 1) the contribution of waterbirds to wels catfish diet in the reserve, 2) the population density of wels catfish in the Reserve and control areas and 3) the potential impacts of waterbird depredation by wels catfish on waterbird population sustainability. We hypothesised that invasive wels catfish predation could be a potentially significant pressure on waterbirds, especially during the nesting season and on chicks. We assumed predation would be predator-density dependent and expected predation to be size-limited, so that young birds would be the main prey and larger wels catfish to have a higher proportion of birds in their diet. Ultimately, our study constitutes a preliminary attempt to assess the potential of introduced wels catfish to affect the conservation value of waterbird protection areas.

Materials and methods

Study setup

To assess the effects of wels catfish predation on birds, we utilised a control/impact approach, assuming that predation would be density-dependent (i.e. that it would be less significant in the control area, where predator density is much lower). We used a preliminary analysis of wels catfish stomach contents to guide our field sampling of their putative prey items. We then estimated the avian contribution to the diet of wels catfish in the Reserve using a stable isotope Bayesian mixing model and its biomass using electrofishing removal. Based on three different bioenergetic models, we estimated wels catfish daily feeding rates and used this information to estimate birds' consumption by wels catfish in the Reserve (impact area) during the nesting and chick growing period (April-June, 90 days) of 2019. We then used mallard (*Anas platyrhynchos*) chick counts in 2017–2019 to compare reproductive success in the control and test areas, to gauge potential differences in predation magnitude and considered reproductive bird trends in the Reserve and surrounding areas to detect any broad effects.

Study area

Our control area consisted in the area where the Oglio River flows into Lake Iseo, about 17.5 km north of the Reserve. Both control and test areas share an equal number

and type of other potential predators (e.g. birds or mammals), but the control area is characterised by high anthropogenic presence, no bird protection measures (i.e. hunting is allowed) and slightly deeper, flowing water. Wels catfish is present in the control area, but at much lower densities than in our test area (this study).

Our test area consisted in the Sebino peat bogs ('Torbiere del Sebino', in Italian), a marshland of ~ 360 ha, located near the southern shore of Lake Iseo (6530 ha), in northern Italy. These bogs are typically shallow (average depth 5 m, this study) and cold-temperate (5.8–28.3 °C during 2019, this study), with abundant emergent and submerged aquatic vegetation and are intermittently connected to the Lake. The *Lamette* part of the bogs is a shallow (max. depth 5 m) marshland with abundant reeds that has the closest connection with the Lake and is a strict Reserve (i.e. no human activities are allowed). Conversely, the 'Torbiere' and 'Lama' parts of the bogs are a series of deeper (max. depth 9 m) lakes, have restricted public access and, in some parts, recreational fishing is permitted (Fig. 1). The Sebino Peat Bog Nature Reserve (hereafter referred to simply as the Reserve) was established in 1984 and is protected under both national and European legislation (Natura 2000 network). Prior to this protection, the bogs were used extensively for peat harvest. The Reserve is a key nesting area for waterbirds, as well as an important stopover area during the migration period and a relevant wintering site (Trotti 2019). Out of the total 268 bird species observed in the Reserve since the 1950s, 14 are introduced and 31 are covered by the EU Birds Directive (Trotti 2019).

Wels catfish were first accidentally introduced to Lake Iseo through the Oglio River and ultimately to the Reserve in the late 1980s (Mancini, unpublished data), but their numbers in the Reserve were initially low and they were not detected until much later. Wels catfish biomass in the Reserve is likely to have increased around 2005–2008, leading first to their detection and then to selective harvest in 2011, to limit the introduced fish population in the Reserve (Mancini, unpublished data).

Fish diet analysis

We assumed that small-sized catfish would not be effective predators of adult and sub-adult birds, due to mouth gape limitations. Therefore, we sampled 31 large-sized wels catfish (total length > 98 cm, hereafter simply referred to as length) by spearfishing in the Reserve during spring-summer 2019. These individuals were analysed for stomach contents using a volumetric point method (Windell 1968) to collect preliminary information on catfish diet and guide sampling of putative prey for stable isotope analysis. Not unexpectedly for predator fish, 20 wels catfish stomachs were found empty and 11 stomachs contained prey, of which four contained red swamp crayfish (39.1% of total combined volumetric contents), three contained unidentified remains (13%), two contained fish of different sizes (Italian rudd, *Scardinius hesperidicus* and unidentified, 13%), one contained a rodent (unidentified, 8.7%), one a feather and one an adult bird (cormorant, *Phalacrocorax* spp., 26.1%).

Based on this guidance and on literature dietary information (e.g. Copp et al. 2009), we sampled catfish muscle from our preliminary sample and a range of putative

prey species from the Reserve for stable isotope dietary analysis. Permits for collection of field samples were obtained from the ‘Torbiere del Sebino’ Nature Reserve administration within the wels catfish control programme, all individuals were immediately euthanised after capture and no protected species were culled in this study. We collected muscle of putative aquatic prey, including large piscivorous fish (three individual samples from two species), small generalist fish (12 individual samples from six species) and alien red swamp crayfish (*Procambarus clarkii*, eight individual samples) through electrofishing. We also collected muscle from putative terrestrial prey, including one rodent muscle (*Rattus* sp. from fish stomach contents) and feather (calamus) samples from several waterbird species (43 individual samples from eight species, from fish stomach contents, birds found dead and natural moulting) through an opportunistic collection. A detailed list of samples and species is provided in Suppl. material 1: Table S1. Collecting feathers allowed for non-lethal sampling of birds, while offering a stable isotope measure comparable to muscle tissue (Hobson and Clark 1992a, b).

Tissue samples were dried at 60 °C, ground to fine powder (muscle) or cut to size (feathers). As lipid variations in tissues can alter $\delta^{13}\text{C}$ values, feathers were rinsed in 2:1 chloroform/methanol solution to remove surface lipids and stable isotopes ratios of C in other tissues were later arithmetically corrected for lipid content (Kiljunen et al. 2006). Samples were analysed for stable isotope ratios of C and N at the University of Jyväskylä, Finland, using a Thermo Finnigan DELTA^{plus} Advantage continuous-flow stable isotope-ratio mass spectrometer (CF-SIRMS), coupled with a FlashEA 1112 elemental analyser (Thermo Electron Corporation, Waltham, MA, USA). The resulting ratios were expressed in terms of relative concentrations relative to a laboratory reference standard. While a rodent and a feather sample collected from stomach contents were isotopically analysed, they were eventually excluded from further analysis to avoid issues with potential consumer contamination and low sample size.

We estimated diet proportions of wels catfish with a Bayesian mixing model under R statistical software 3.6 (R Core Team 2019) through the mixSIAR package (Stock et al. 2018), which accounts for sample size when estimating diet proportions and using literature isotope fractionation [$\delta^{13}\text{C} = 0.4 \pm 1.2$, $\delta^{15}\text{N} = 2.3 \pm 1.6$, (McCutchan et al. 2003)]. We tested for wels catfish size effects by running a mixing model where catfish length was considered as a continuous covariate, after testing that differences in diet composition between size classes suggested by our preliminary stomach content analysis were not significant in the isotopic space (PERMANOVA P-value > 0.05). We also used our preliminary stomach content analysis and expert judgement to produce informative priors (see Suppl. material 1: Fig. S3) that were used in the mixing model (Moore and Semmens 2008), with a very conservative approach to bird consumption values. We additionally ran re-sample simulations (100 iterations each for samples sizes 2–50) to assess isotopic sources sample size effects on the results of the model, using the package ‘samplesim’ (Casajus et al. 2021). Putative prey species were divided into five functional groups (Small fish, Large Fish, Crayfish, Invertivorous Birds, Herbivorous Birds and Piscivorous Birds), based on taxonomy and ecology. The piscivorous birds included cormorants and grebes (thus with both a marine and freshwater signal),

the herbivorous birds included swans, mallards, pochards and moorhens and the invertivorous birds included water rails. Chicks of most waterbird species are invertivorous during growth (Sugden 1973), but no specific groups were created for chicks.

Fish biomass estimation

To estimate wels catfish biomass in the Reserve, we used 73 boat-mounted electrofishing events between 2013 and 2019, covering the shoreline of all three main areas of the Reserve ('Lama', 40 events, 'Lamette', 23 events, 'Torbier', 10 events) and all seasons (but focusing on autumn and spring). A total of 1356 individuals were caught and removed from the Reserve using electrofishing, for an overall weight of 8113 kg. Wels catfish were of average total length 84.45 cm (median 82 cm, min. 2.2/max. 211 cm) and of average weight 5.98 kg (median 3.84 kg, min. 0.015/max. 92.75 kg).

We estimated the overall biomass of wels catfish in each of three areas of the Reserve, by averaging the detected density at each sampling event. Density was calculated as a function of biomass harvested and area sampled during each event, where area was the length of the shoreline fished, multiplied by the effective radius of the electrofisher (i.e. 5 m). Density trends over time were analysed with linear regressions. Given that we only estimated density in shoreline areas and that electrofishing catchability is high but not perfect, ours was likely an underestimation of total biomass.

To estimate wels catfish biomass in the control area, we used a boat-mounted electrofishing survey followed by three visual census surveys, carried out between 2012 and 2016 and spanning from April to July, along the shorelines of the control area (including the terminal part of the Oglio River).

Wels catfish consumption models

We estimated wels catfish annual consumption of prey by developing a specific bioenergetic model for the local conditions and sampled size cohorts. We used the Wisconsin bioenergetic model (Hanson et al. 1997), parametrised according to experimental studies on wels catfish and similar species (Hilge 1985; Raat 1990; Xiao-Jun and Ruyung 1992; Bourret et al. 2008, see Suppl. material 1: Table S2) to estimate annual consumption. Fish being poikilotherms, the model relies on water temperature to assess metabolic rates and on prey energy content to model body mass gain. We thus used records of daily average temperatures in the Reserve in 2019 (when catfish were sampled, see Suppl. material 1: Fig. S1), food energy contents from Cummins and Wuycheck (1971) (see Suppl. material 1: Table S3) and diet composition derived from our stable isotope analysis as inputs to the model. We used model results to calculate an average daily consumption of wels catfish during the chick growing period, accounting for site-specific diet composition, size and growth (see Suppl. material 1: Table S3), estimated based on yearly length increments from Rossi et al. (1991). Weight increments were derived from length, using a weight/length regression fitted to our data ($W = 7E-05 * L^{2.6535}$, $R^2 = 0.9374$).

Additionally, we compared our model results with two previous consumption estimates. An average daily consumption of 1.99% of wet mass day⁻¹ was estimated by Omarov and Popova (1985) and Orlova and Popova (1986) for wels catfish in Georgia over the whole year. A similar value of 1.32% of wet mass day⁻¹ was also estimated by Copp et al. (2009) in their review, also including European data.

We then used the estimated biomass and the three different estimates of average daily consumptions listed above to calculate the total quantity (kg) of prey ingested over a year. The consumption of bird prey was then estimated, based on its dietary proportion, as estimated by our stable isotope mixing models, accounting for the error in the dietary contribution (50% confidence interval) and in the biomass estimate (SD around the mean) when calculating the upper and lower confidence limits of the consumption estimate. Bird consumption was estimated exclusively for the > 98 cm size cohort, as diet was determined only for this size class.

Bird abundance and trends

We used nesting bird surveys from 2002–2019 (Brichetti 2002; Longo 2009; Trotti et al. 2016; Trotti 2017, 2018, 2019) to assess the consistency and short-term trends of waterbirds (i.e. ecologically dependent upon wetlands) nesting in the Reserve, which could be potential prey for wels catfish. Surveys were carried out by 1–3 experienced observers, between May and September, for a total of more than 30 days per year. Surveys included nestling and chick counts during and after the breeding season and were performed from both shore and boats, at dawn and dusk. We focused on nesting birds, as young birds are smaller and likely to be more readily predated and the breeding season coincides with the period of warmer temperatures, which increase fish activity and thus predation. Given the few data points, trends in nesting birds numbers were identified using simple linear regressions and given a qualitative classification as Stable (coefficient < 0.2), Moderate increase/decrease (0.2 < coefficient < 0.5) and Increase/Decrease (0.5 < coefficient), reporting only R² values. Additionally, long-term trends in wintering numbers estimated by the International Wetland Census for the functional/ecological spatial wintering unit that includes the study area, plus contiguous spatial units (Zenatello et al. 2014) were also retrieved for comparison of local and larger spatial scale trends.

To offer a comparison of the scale and potential impact of wels catfish consumption on birds, we used average weights of each bird species (accounting for sexual dimorphism in size, see Suppl. material 1: Table S4) to estimate an overall nesting adult biomass in the Reserve during the summer season (i.e. the season when fish predation is most likely). We may have underestimated the total waterbird biomass because we did not include the weight of chicks and there may be constant turnover of individuals in the bird population. Furthermore, the waterbird biomass would be considerably higher in winter, when bird numbers increase.

Finally, we used reproductive success surveys, carried out in 2017–2019 with similar methods as the nesting bird surveys, to assess differences in the number of chicks

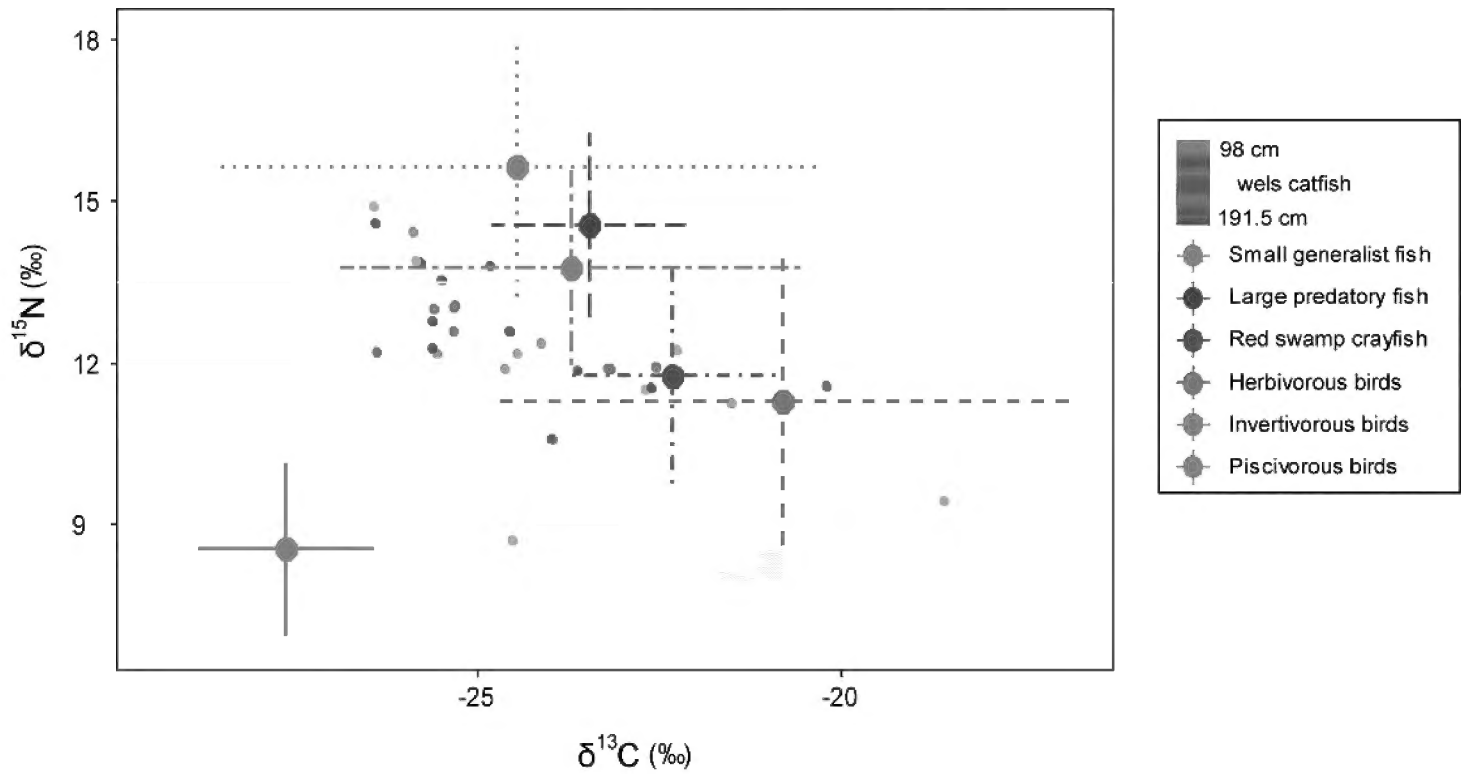


Figure 2. Isotopic space positions of wels catfish and its putative prey sources in the Reserve, corrected for isotopic fractionation. Error bars represent standard deviations of each prey source. Feathers were analysed for birds and muscle for other taxa; both were corrected for lipid content.

per couple of waterbirds in the control and the Reserve areas. We chose mallard as a test species, as it is a cosmopolitan and abundant species in both areas and counted the number of chicks per couple in early (mid-April/mid-May) and late (June) stages of the chick growing period in order to test differences in the median number of chicks at the late stage across the areas and differences in the slopes between early and late stages across areas, under the null hypotheses that different areas would have equal means and slopes. We used the non-parametric Mann-Whitney test on the medians and the test on the difference between the slopes from two independent samples outlined in Howell (2012).

Results

Fish diet

Wels catfish in our sample ($n = 30$, mean 139.9 cm, SD 30.5 cm, length range 98–191.5 cm) were generally spread between sources in isotopic space (Fig. 2), but there were no clear trends stemming from wels catfish length in the mixing model.

The Bayesian mixing model indicated that birds composed 12.2% (5–27.9%, 50% confidence interval) of the diet of wels catfish > 98 cm in length. More specifically, invertivorous bird prey composed 8.6% (4.6–14.1%, 50% confidence interval) of the diet, while herbivorous and piscivorous bird prey composed 1.7% (0.2–6.4%, 50% confidence interval) and 1.9% (0.2–7.4%, 50% confidence interval) of the diet, re-

spectively (Fig. 3). According to the mixing model, larger catfish did not have a higher proportion of birds in their diet.

Our sample size simulation indicated that increasing sample size up to 50 samples was likely to downplay the dietary proportions of crayfish and large fish and increase the relevance of birds (particularly piscivorous birds) by up to ~ 5%, but not to decrease the width of confidence intervals, except for invertivorous birds (see Suppl. material 1: Fig. S4a, b). Doubling wels catfish sample size would have similarly yielded a ~ 10% increase in the relevance of birds (particularly invertivorous birds) and a similar decrease of the width of confidence intervals (see Suppl. material 1: Fig. S4c).

Fish biomass

Detected wels catfish density ranged 3.4–174 kg/ha, with highest densities recorded in the ‘Lama’ part of the Reserve and no clear trends were observed in 2013–2019 (see Suppl. material 1: Fig. S2). The estimated average total biomass of wels catfish (of all sizes) along the Reserve shorelines was 1237 (\pm 254) kg. Despite being only 22.9% of the total individuals sampled, fish 98–191 cm of length were estimated to have an average biomass of 1024 kg, 83% of the total biomass.

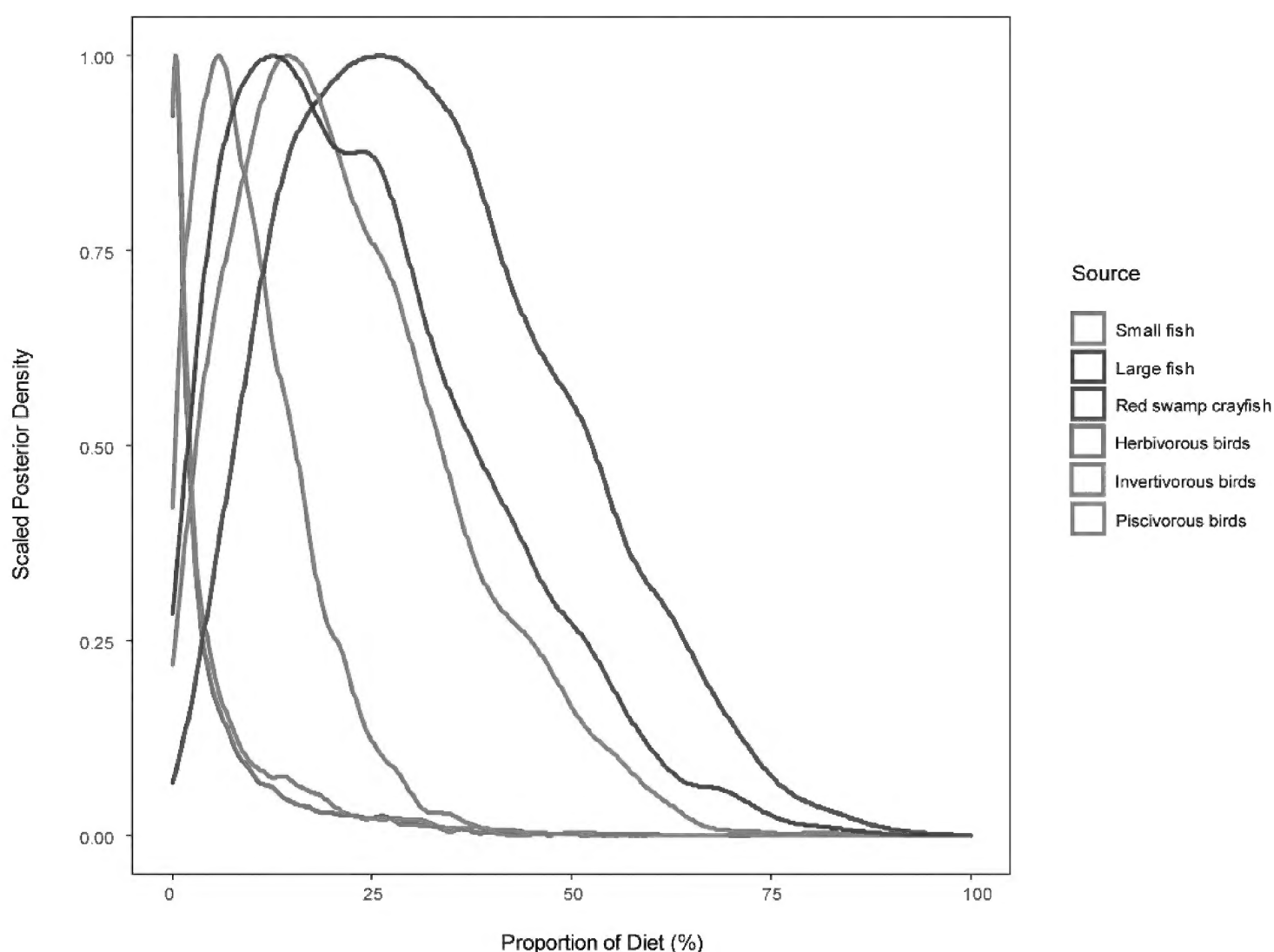


Figure 3. Curves of dietary proportions of wels catfish prey sources, derived from the Bayesian mixing model for stable isotopes including weakly informative dietary priors.

None of the surveys in the control area was able to detect wels catfish, despite covering a total combined surface of 75.7 km². We thus conservatively concluded that, albeit present in Lake Iseo, wels catfish density in the control area was below detectable levels and, thus, likely to be negligible compared to the biomass detected in the Reserve.

Bird consumption

Our bioenergetic model suggested an average daily ratio of 1.7% wet mass day⁻¹ for a wels catfish > 98 cm during the chick growing period (and an average daily ratio of 1.5% wet mass day⁻¹ over the whole year).

The estimated average bird consumption for the wels catfish population > 98 cm during the chick growing period was 224, 148 and 187 kg, respectively, as estimated through the three different daily ratios (Fig. 4). By comparison, the overall biomass of the 243 waterbird nesting pairs in the Reserve during 2019 was estimated at 792 kg (691 kg excluding adult swans, Fig. 4).

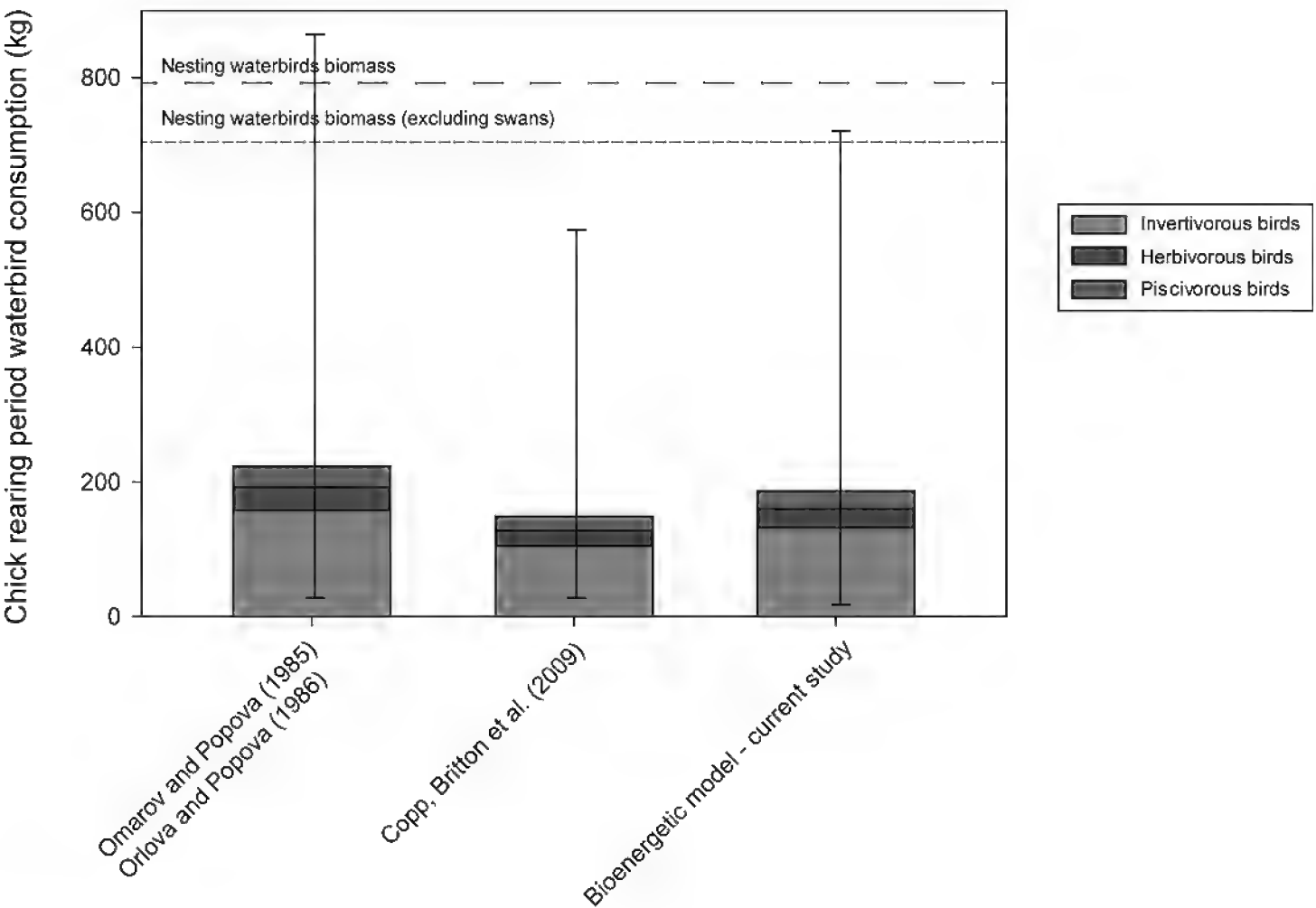


Figure 4. Estimated consumption of birds by wels catfish in the shoreline of the Nature Reserve during the chick growing period of 2019, as obtained with the three different estimates of daily consumption ratios. Error bars account for uncertainty in both dietary and biomass estimations. The horizontal dashed lines indicate the estimated biomass of nesting adult waterbirds observed in the Reserve during the chick growing period of 2019.

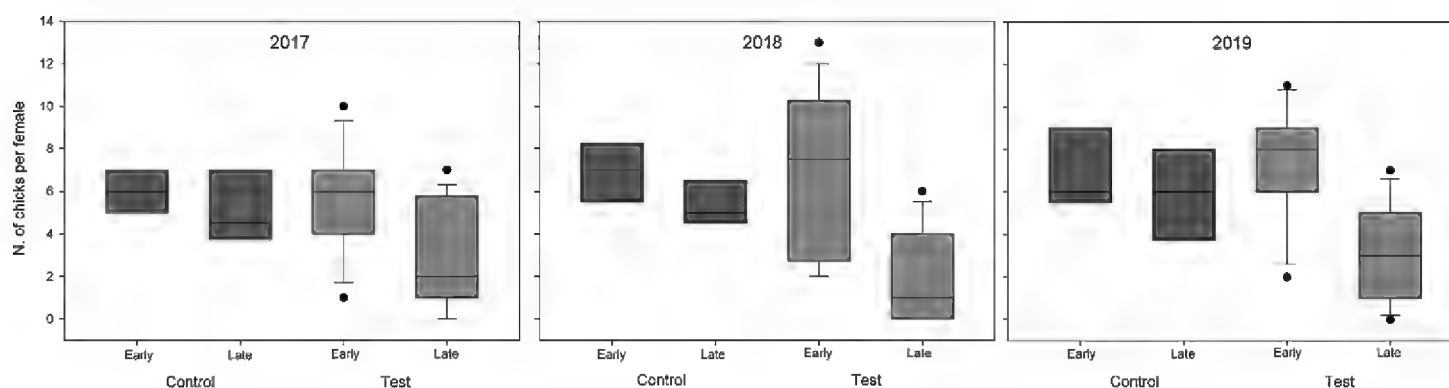


Figure 5. Mallard chicks per pair in the control (green) and test (orange) areas, as detected in early (mid-April/mid-May) and late (June) stages of the chicks growing period. In boxplots, black horizontal lines represent medians, boxes represent the first and third quartile, whiskers represent minimum and maximum values and dots represent extreme values.

Bird population trends

A total of 12 waterbird species that could be potential prey of wels catfish were found nesting in the Reserve in 2002–2019, for a total of 243 nesting pairs. The most abundant breeding species was the great cormorant (*Phalacrocorax carbo*, 83 breeding pairs), while the least abundant was the mute swan (*Cygnus olor*, five breeding pairs). The number of breeding pairs was generally consistent in 2017–2019 for most species (Table 1), increasing for some species (e.g. the great cormorant), but markedly lower than those detected in 2002 for other species (e.g. Eurasian coot, *Fulica atra*). The total estimated nesting waterbird biomass in 2019 was 792 kg (691 kg, excluding adult swans which are particularly large prey).

During 2017–2019, mallard reproductive success at early stages of the chick growing period was equal in the test rather than in the control area (Fig. 5, Mann-Whitney P-value > 0.7 for all years). However, in 2018 and 2019, there were statistically significant differences between the test and control areas in the number of chicks at late stages of the growing period (Mann-Whitney P-values < 0.01 and < 0.05, respectively), even if those were not significant in 2017 (Mann-Whitney P-value = 0.06). The differences in slopes expressing the rate of decline were statistically significant in 2018 (P-value < 0.03), but not in 2017 and 2019 (P values 0.3 and 0.06, respectively).

Discussion

Regarding objective 1, our analysis confirmed that the diet of the wels catfish population in the Reserve included birds, albeit their median diet proportion (12.2%) was not as high as in a previous study that focused on specialised individuals (Cucherousset et al. 2012). As for objective 2, we found the shoreline areas of the Reserve hosted a population composed mainly of large (> 98 cm) wels catfish and its biomass (1024 kg) was stable in 2013–2019 despite population control efforts, while wels catfish biomass in the control area was below detectable levels. For objective 3, we found that these fish consumed a relatively small portion of birds during the chick growing period, as estimated

through different daily ratios using the median diet proportion of birds. According to our data (Table 1), for some of the species of waterbirds exposed to fish predation when breeding, the number of nesting couples declined after wels catfish was detected in the Reserve and stabilised to lower levels after that. Additionally, compared to the control area, mallard reproductive success was diminished in the Reserve, even if effects were variable in different years. This appears to be the case for precocial birds, such as waterfowl, coots and grebes that rear their young on the water, but not for altricial herons and cormorants which rear their young in the nest (Table 1). Overall, our data suggest that high densities of invasive wels catfish might impact waterbird reproductive success through predation on bird chicks, but further studies would be needed to reduce uncertainties related to the intrinsic limitations of field ecology. Ultimately, our study constitutes a preliminary attempt to assess the potential of introduced wels catfish to affect the conservation value of waterbird protection areas and further investigation is required.

Fish diet composition is often driven by prey availability, while fish dietary intake is a function of activity and metabolism, which are mostly driven by body size and temperature, so uncertainties might be compounded in the final estimate of predation effects. Cucherousset et al. (2012) found that the bird component of wels catfish diet could be important for individuals specialising on pigeon predation. Our stable

Table 1. Numbers of nesting waterbird pairs of each species that could be potential prey of wels catfish in the Reserve, 2002–2019 and their local trends (based on at least three years of data). For comparison, the last column lists long-term trends in wintering numbers estimated by the International Wetland Census for the functional/ecological spatial wintering unit that includes the study area, plus contiguous spatial units (Zenatello et al. 2014). The vertical red line marks the period when wels catfish were first detected in the Reserve (2005–2008). Bold common names highlight species that were sampled for stable isotopes in our study, + indicates species present, but not counted.

Common name	Scientific name	2002	2009	2016	2017	2018	2019	Local trend	IWC National Winter Trend
Mute swan	<i>Cygnus olor</i>	+	16	+	5	5	5	Decrease ($R^2 = 0.97$)	Increase
Great cormorant	<i>Phalacrocorax carbo</i>	+	+	41	52	75	83	Increase ($R^2 = 0.97$)	Moderate increase
Red-crested pochard	<i>Netta rufina</i>	+	+	+	7	6	8	Moderate increase ($R^2 = 0.25$)	Increase
Eurasian coot	<i>Fulica atra</i>	20	9	+	7	10	10	Decrease ($R^2 = 0.63$)	Moderate increase
Common moorhen	<i>Gallinula chloropus</i>	+	+	+	50	50	50	Stable ($R^2 = 1$)	Moderate increase
Mallard	<i>Anas platyrhynchos</i>	20	+	+	21	20	20	Stable ($R^2 = 0.96$)	Increase
Great crested grebe	<i>Podiceps cristatus</i>	35	+	+	22	12	13	Decrease ($R^2 = 0.88$)	Moderate increase
Little grebe	<i>Tachybaptus ruficollis</i>	+	+	+	6	7	8	Moderate increase ($R^2 = 1$)	Moderate increase
Water rail	<i>Rallus aquaticus</i>	+	+	+	3	6	8	Moderate increase ($R^2 = 1$)	Increase
Purple heron	<i>Ardea purpurea</i>	6	+	+	8	12	9	Moderate increase ($R^2 = 0.56$)	Not wintering in Italy
Little bittern	<i>Ixobrychus minutus</i>	5	+	+	7	10	10	Moderate increase ($R^2 = 0.75$)	Not wintering in Italy
Black-crowned night heron	<i>Nycticorax nycticorax</i>	50	17	10	15	27	19	Decrease ($R^2 = 0.53$)	Moderate increase

isotope data suggest that bird prey might not be limited to a few individuals with specialised predatory behaviour. However, both studies suffered from relatively low sample size of putative prey, which our analysis indicated could be downplaying the proportion of birds in catfish diet. Future studies should strive to increase putative prey sample size, aiming to get at least 15–25 stable isotope samples per prey category, but this might not yield a significant gain in the final estimate and may prove very challenging for some prey categories (e.g. birds). Sampling would also need to take into account the spatio-temporal variation in isotopic signals (Perga and Gerdeaux 2005) and the pulsed nature of prey sources (e.g. seasonal presence of breeding birds), by appropriately targeting sampling across space and time. Our simulations on sample size effects indicated that higher sample size would not dramatically decrease uncertainty around median estimates of diet proportions and that the bird component of the diet is likely to remain consistent with our findings. Additionally, our bioenergetic model yielded similar consumption ratios as previously reported in literature. In any case, these two components make minor contributions overall to the uncertainty in bird consumption estimates. Uncertainties in the estimate of predator biomass remain the major source of error in the consumption estimate, but these might be a feature of field sampling and are unlikely to be reduced by increasing sampling effort, as this study already used a high number of sampling and removal events.

A more robust study setup, including further replicates of control and test areas, would be needed before drawing firm conclusions, but dietary proportions cannot be easily transposed from one area to another, so area-specific dietary studies would exponentially increase the fieldwork load. Adding replicates will also likely face a challenge in finding predator-free areas where the confounding effects of predator density could be excluded altogether. Wels catfish is currently widespread in Italian freshwaters, has heavily colonised the drainage of all main rivers in the country (Po, Arno, Tevere and Volturno Rivers) and is present in most of the protected areas of northern and central Italy. Where present, it tends to dominate the community of predator fishes (~ 30% of the whole fish community biomass, M. Milardi, unpublished data). Wels catfish and other introduced fish species are a major problem also for native fish diversity in Italian freshwaters (Milardi et al. 2018, 2019a, 2020a, 2020b, 2020c), but to date, little has been done to address this problem. A recent review by Cucherousset et al. (2018) underlined how the species is widespread and abundant also in the rest of its introduced range (e.g. France and Spain), where it was shown to have impacted on native fish, especially during migrations (Boulêtreau et al. 2020a, 2020b).

Local bird populations trends could be driven by population dynamics at a larger spatial scale (Milardi et al. 2019b). We tried to account for this uncertainty by considering the most recent assessment of long-term wintering population trends at the national scale (up to 2010), which highlighted how most waterbird species in our study area have trends decoupled from wider dynamics (Zenatello et al. 2014). This pattern was even more evident when examining the time series available for functional/ecological wintering units including our study area or in contiguous units, which all showed similar trends, suggesting that local-scale drivers, rather than larger-scale drivers, are driving local dynamics during the breeding season. Invasive freshwater predators have greater effects

than terrestrial ones because of native prey naïveté (Cox and Lima 2006) and the lack of experience with intense predation by introduced aquatic predators could partially explain why waterbirds are still nesting in our study site, despite the predation risk. Prey naïveté is less likely to apply to waterbirds given their mobility, as individuals may move to and from the native area of wels catfish, so predation avoidance strategies may be learned in or inherited from the native area (in a manner impossible for naïve fish prey). However, both native and introduced aquatic predator strategies are likely to be similar and waterbirds might have limited capabilities to learn or deploy effective antipredator behaviour (e.g. because they are unable to detect large sit-and-wait predatory fish by sight or smell).

At present, it is still unclear whether all bird species could learn to avoid areas with high predation risk and, therefore, low reproductive success, as found for waterfowl exposed to northern pike predation (Dessborn et al. 2011). If most areas are heavily invaded, birds might have no choice but to try and breed where the catfish are, irrespective of their ability to gauge risks. If conservation areas are invaded, they might attract birds because of the perceived protection from human disturbance or suitable nesting habitat, yet ultimately, turn to sinks that lower waterbird species' reproductive success through predation by invasive fish. Other invasive fish species present in conservation areas can also have non-predatory effects on waterbirds through trophic cascades and habitat alteration (Maceda-Veiga et al. 2017; Milardi et al. 2020c). Despite their size, small reserves have potentially large conservation benefits (Volenec and Dobson 2020), but our results suggest that wels catfish might impact waterbird reproductive success through predation on bird chicks even in these areas. In our study area, wels catfish density did not decrease despite population control operations, which likely means that immigration of new individuals from Lake Iseo and growth and reproduction of individuals already in the Reserve, balanced the removal effort. However, it is likely that this effort has halted the invasion of wels catfish in the Reserve, mitigating the effects of predation on birds which were evident in the decline detected for some nesting species of waterbirds after the invasion onset. This suggests that post-invasion management is particularly challenging and highlights the value of non-permanent wetlands where periodic droughts offer the possibility to eliminate invasive fish and prevent recolonisation through mesh gates. Ultimately, our study suggests the need for an assessment of wels catfish impact on the conservation value of bird reserves and for more effective measures to mitigate this impact in its introduced range.

Acknowledgements

This research did not receive any specific grant from funding agencies in the public, commercial or not-for-profit sectors. We acknowledge the Nature Reserve administration and, in particular, the *Gruppo Ricerche Avifauna*, for cooperation during field sampling. We also acknowledge Massimo Buizza, Oglio River Consortium, for providing water temperature data. Finally, we would like to acknowledge the help of Marco Zenatello, ISPRA, for his guidance on national bird counts.

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Supplementary material I

Figures and Tables

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Data type: Docx file.

Explanation note: **Figure S1.** Daily average water temperature in the ‘Torbiere del Sebino’ Reserve in 2019. **Figure S2.** Wels catfish density trends detected through sampling events along the shoreline of different areas of the ‘Torbiere del Sebino’ Reserve in 2013–2019, using boat-mounted electrofishing. Each dot represents a single sampling event. **Figure S3.** Comparison between uninformative (right) and informative (left) priors. Informative priors were derived from our preliminary stomach content analysis and were tuned into hyperparameters which were rescaled to have the same mean, but different variance, keeping the relative contributions the same. **Figure S4.** Sample size effects on the width of credible intervals and medians of posterior distributions for the 6 prey categories used in the mixing model. Putative prey sample size, expressed as values (boxplots, a) and percentage change in values (dot and line plots, b). Consumer sample size, expressed as percentage change in values (dot and line plots, c). **Table S1.** Length, weight, stable isotope ratios of C and N and percentage of each element and their ratio, for all the specimens sampled in this study. **Table S2.** Species-specific consumption, respiration and egestion/excretion parameters of the Wisconsin bioenergetic model for wels catfish used in our study. **Table S3.** Full model parameters for the Wisconsin bioenergetic model for wels catfish used in our study. Energy and water content of predator and prey items (Cummins and Wuycheck (1971), see Suppl. material 1: Table S3), dry weight to wet weight conversion factors (Hanson et al. 1997; Hartman and Brandt 1995), start and end weights for each cohort modelled, as well as cohort-specific dietary proportions derived from the stable isotope mixing models. **Table 4.** Average weight of adult males and females of each waterbird species nesting in the Reserve.

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Link: <https://doi.org/10.3897/neobiota.72.80500.suppl1>